



Lemma micromorphological characters in the Chloridoideae (Poaceae) optimized on a molecular phylogeny

Q. Liu ^{a,b,*}, D.X. Zhang ^a, P.M. Peterson ^b

^a Key Laboratory of Plant Resources Conservation and Sustainable Utilization, South China Botanical Garden, the Chinese Academy of Sciences, Guangzhou 510650, China

^b Department of Botany, Smithsonian Institution, Washington DC 20013-7012, USA

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Abstract

Eight lemma micromorphological characters of 83 taxa representing 61 genera in the Chloridoideae have been investigated using Scanning Electron Microscopy, including long cells, cork cells, stomata, bicellular microhairs, papillae, silica cells, micropickles, and macrohairs. Five new types of lemma micromorphological characters were reported here. Data for 27 taxa representing 19 genera from previous publications were also supplied to access the homology of lemma micromorphological characters for different groups through optimization onto a molecular cladogram. Given the optimization, five characters including long cells, cork cells, stomata, papillae, micropickles are of phylogenetic significance for supra-generic groups. Seven characters including straight outline long cells, crescent-shaped cork cells, absent stomata, absent papillae, dumb-bell-shaped silica cells, c-type micropickles, and papillate-base macrohairs may not be homologous, however, the enneapogonoid-type bicellular microhairs appeared as a synapomorphy for the Chloridoideae.

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Keywords: Character; Chloridoideae; Lemma micromorphology; Poaceae; Synapomorphies

1. Introduction

Chloridoideae comprises approximately 140 genera and 1420 species, whose adoption of efficient C₄ photosynthesis has led to its successful proliferation in the tropics and subtropics (Watson and Dallwitz, 1992; Clayton et al., 2008). Taxonomic history clearly shows that it is difficult to recognize monophyletic supra-generic groups within the subfamily (Jacobs, 1986; Kellogg and Campbell, 1987; Davis and Soreng, 1993; Clark et al., 1995; Van den Borre and Watson, 1997; GPWG, 2001; Liu and Zhao, 2004; Columbus et al., 2007; Soreng et al., 2009). For example, the central issue has been whether to

recognize the traditional tribes Cynodonteae and Eragrostideae (Clayton and Renvoize, 1986; Soreng et al., 2009; Peterson et al., *in review*) as distinct. Several attempts have been made to address the phylogenetic relationships in Chloridoideae based on morphological and molecular evidence (Hilu and Wright, 1982; Hilu and Alice, 2001; Liu et al., 2005a,b; Columbus et al., 2007; Peterson et al., 2007a), the phylogenetic patterns of these studies rejected the traditional circumscriptions of Cynodonteae and Eragrostideae.

The importance of lemma micromorphological characters for assessing phylogenetic relationships from species level to tribal level, has been well established in some clades of Poaceae (Terrell and Wergin, 1981; Vignal, 1984; Thomasson, 1986; Peterson, 1989; Valdés-Reyna and Hatch, 1991; Snow, 1996; Mejia-Saules and Bisby, 2003; Bell and Columbus, 2008). While in Chloridoideae, except for descriptive studies of closely related genera in the tribe Eragrostideae (Valdés-Reyna and Hatch, 1991; Snow, 1996), little is known about the phylogenetic implications of lemma micromorphological characters

* Corresponding author. Key Laboratory of Plant Resources Conservation and Sustainable Utilization, South China Botanical Garden, the Chinese Academy of Sciences, Guangzhou 510650, China. Tel.: +86 20 37252567.

E-mail address: liuqing@scib.ac.cn (Q. Liu).

Table 1

Chloridoideae material studied (following the classification of Soreng et al., 2009; Peterson et al., in review).

Tribe/subtribe	Species	Country	Voucher	Figure(s)
<i>Incertae Sedis</i>				
	<i>Tetrachaete elionuroides</i> Chiov.	Tanzania	Peter 13516 (K)	52
	<i>Farrago racemosa</i> Clayton	Tanzania	Anderson 1150 (K)	50
	<i>Oropetium thomaeum</i> (L. f.) Trin.	India	Koenig s.n. (LINN)	–
	<i>Odysea paucinervis</i> (Nees) Stapf	Ethiopia	Schimper 1652 (P)	20
	<i>Halopyrum mucronatum</i> (L.) Stapf	Kenya	Polhill & Paulo 766 (K)	–
	<i>Leptocarydion vulpiastrum</i> (DeNot.) Stapf	Kenya	Gillett 13107 (K)	–
	<i>Drake–Brockmania somalensis</i> Stapf	Kenya	Greenway 9201 (K)	21
	<i>Psilolemma jaegeri</i> (Pilg.) S.M. Phillips	Tanzania	Jaeger 320 (B)	43
	<i>Desmostachya bipinnata</i> (L.) Stapf	China	Guoai Fu 6038 (IBSC)	42
	<i>Daknopholis boivinii</i> (A. Camus) Clayton	Madagascan	B. Oivin 2288 (P)	–
	<i>Leptothrium senegalense</i> (Kunth) Clayton	Kenya	Gillett 12992 (K)	–
	<i>Habrochloa bullockii</i> C.E. Hubb.	Tanzania	Webster T. 234 (K)	–
	<i>Chrysochloa hindsii</i> C.E. Hubb.	Tanzania	Webster T. 39 (K)	–
<i>Triraphideae</i>				
<i>Triraphidinae</i>				
	<i>Triraphis schinzii</i> Hack.	Tanzania	Semsei 1325 (K)	–
	<i>Neyraudia reynaudiana</i> (Kunth) Keng ex Hitchc.	USA	Brooks 1045 (US)	28
		China	Binggui Li 5330 (IBSC)	18
<i>Eragrostideae</i>				
<i>Cotteinae</i>				
	<i>Enneapogon desvauxii</i> P. Beauv.	Cape Province	Smook L. 8570 (IBSC)	9,45,51
	<i>Schmidtia pappophoroides</i> Steud. ex J.A. Schmidt	Uganda	Eggeling 5819 (K)	7,19
<i>Uniolinae</i>				
	<i>Uniola paniculata</i> L.	USA	Jackson E.N.S. 4256 (IBSC)	–
	<i>Fingerhuthia africana</i> Nees ex Lehm.	Cape Province	Hayden & Johnson 136 (IBSC)	36
<i>Eragrostidinae</i>				
	<i>Eragrostis atrovirens</i> (Desf.) Trin. ex Steud.	China	Guoliang Shi 15328 (IBSC)	–
	<i>E. cilianensis</i> (All.) Vignolo ex Janch.	China	Ceming Tan 99555 (IBSC)	8
	<i>E. ciliata</i> (Roxb.) Nees	China	Shaoqing Chen 11076 (IBSC)	–
	<i>E. cylindrica</i> (Roxb.) Nees ex Hook. & Arn.	China	Xuwen Wang 331 (IBSC)	–
	<i>E. tenella</i> (L.) P. Beauv. ex Roem. & Schult.	China	Shaoqing Chen 11076 (IBSC)	–
	<i>Pogonarthria squarrosa</i> (Roem. & Schult.) Pilg.	South Africa	Lichtenstein (B)	–
	<i>Harpachne schimperii</i> Hochst ex A.Rich.	Tanzania	Richards 25175 (K)	–
<i>Zoysieae</i>				
<i>Zoysiinae</i>				
	<i>Zoysia japonica</i> Steud.	China	Rui Wang 007 (IBSC)	25,49
<i>Sporobolinae</i>				
	<i>Sporobolus tenuissimus</i> (Mart.ex Schrank) Kuntze	France	Homburg 80 (IBSC)	40
	<i>S. virginicus</i> (L.) Kunth	China	Binghui Chen 355 (IBSC)	41
	<i>S. fertilis</i> (Steud.) Clayton	China	Qing Liu 021 (IBSC)	–
	<i>Crypsis aculeata</i> (L.) Aiton	China	Fangdong Liu 10332 (IBSC)	57
	<i>C. schoenoides</i> (L.) Lam.	Spain	Löfing s. n. (LINN)	–
	<i>Spartina alterniflora</i> Loisel.	China	Kinshen Hao 3437 (IBSC)	17,27,58
	<i>S. anglica</i> C.E.Hubb.	China	Binghui Chen 773 (IBSC)	48
	<i>Pogoneura biflora</i> Napper	Tanzania	Greenway 10620 (K)	11
<i>Cynodonteae</i>				
	<i>Bewisia biflora</i> (Hack.) Gooss.	Tanzania	Webster T. 59 (K)	23
	<i>Ctenium newtonii</i> Hack.	Uganda	Buechner 129 (K)	–
	<i>Eragrostiella bifaria</i> (Vahl) Bor	Kenya	Bogdan 3360 (K)	–
	<i>Dactyloctenium aegyptium</i> (L.)P.Beauv.	China	Qing Liu 042 (IBSC)	12,38
	<i>D. australe</i> Steud.	Tanzania	Batianoff 1261 (IBSC)	–
	<i>Trichoneura ciliata</i> (Peter) S.M.Phillips	Tanzania	Greenway 10196 (K)	–
	<i>Orinus thoroldii</i> (Stapf ex Hemsl.) Bor	China	Exp. Jinsha River 6444 (KUN)	30,47
	<i>Cleistogenes longiflora</i> Keng ex Keng f. e& L.Liou	China	Anren Li 6250 (IBSC)	2,13,46
	<i>C. hackelii</i> (Honda) Honda	China	Linhan Liu 16443 (IBSC)	55
	<i>C. chinensis</i> (Maxim.) Keng	China	Yourun Lin 83–82 (IBSC)	56
	<i>C. caespitosa</i> Keng	China	Exp. Huang Mt. 818 (IBSC)	–
	<i>Acrachne racemosa</i> (B.Heyne ex Roem. & Schult.) Ohwi	China	Xinqi Liu 27579 (IBSC)	–
	<i>Dignathia gracilis</i> Stapf	Kenya	Greenway 9497 (K)	–
<i>Triodiinae</i>				
	<i>Triodia irritans</i> R. Br.	Australia	Jackson E. N. S. 4243 (IBSC)	14,31
	<i>T. lanata</i> J. M. Black	Australia	Jackson E. N. S. 4256 (IBSC)	–
<i>Aluopodinae</i>				
	<i>Aeluropus littoralis</i> (Gouan) Parl.	China	Smook L. 8500 (IBSC)	37
	<i>A. littoralis</i> Parl. subsp. <i>sinensis</i> (Debeaux) Tzvelev	China	Kejian Guan 868 (IBSC)	33
<i>Eleusininae</i>				
	<i>Apochiton burttii</i> C. E. Hubb.	Tanzania	Glover 1 (K)	32
	<i>Leptochloa fusca</i> (L.) Kunth	China	Fangdong Liu 11076 (IBSC)	10,29
	<i>L. chinensis</i> (L.) Nees	China	Exp. Longxi Mt. 2151 (IBSC)	60
	<i>Dinebra retroflexa</i> (Vahl) Panz.	China	Zhihao Hu 7900749 (PE)	–

(continued on next page)

Table 1 (continued)

Tribe/subtribe	Species	Country	Voucher	Figure(s)
	<i>D. polycarpha</i> S.M. Phillips	Kenya	Bogdan 3918 (K)	–
	<i>Coelachyrum longiglume</i> Napper	Kenya	M. Senyimba 365 (K)	34
	<i>Eleusine indica</i> (L.) Gaertn.	China	Dingyi Peng 46843 (IBSC)	–
	<i>E. coracana</i> (L.) Gaertn.	China	Qing Liu 028 (IBSC)	–
	<i>Lepturus repens</i> (G. Forst.) R.Br.	China	Zexian Li 5374 (IBSC)	–
	<i>Enteropogon dolichostachyus</i> (Lag.) Keng ex Lazarides	Australia	Thompson BUC 733 (IBSC)	35
	<i>Microchloa indica</i> (L.f.) P. Beauv.	China	Heyun Mai 20246 (IBSC)	15,26,39
	<i>M. altera</i> (Rendle) Stapf	Tanzania	Procter 2442 (K)	–
	<i>Cynodon arcuatus</i> J. Presl	China	Qing Liu 015 (IBSC)	16
	<i>Brachyachne patentiflora</i> (Stent & Rattray) C.E. Hubb.	Kenya	Bogdan 4075 (K)	–
	<i>Schoenefeldia transiens</i> (Pilg.) Chiov.	Tanzania	Vhlig 982 (B)	–
Monanthochloinae	<i>Distichlis spicata</i> (L.) Greene	China	Zhenwan Zhang 436 (IBSC)	–
Muhlenbergiinae	<i>Muhlenbergia japonica</i> Steud.	China	Tianlun Dai 103515 (IBSC)	–
	<i>M. curvيارistata</i> (Ohwi) Ohwi	China	Yanchang Wang 785 (IBSC)	–
Boutelouinae	<i>Bouteloua curtipendula</i> (Michx.) Torr.	China (Introduced)	Zhenwan Zhang 593 (IBSC)	3
Tragaineae	<i>Tragus australianus</i> S.T. Blake	Australia	Badman 1848 (IBSC)	53,54
	<i>T. berteronianus</i> Schult.	China	Fangdong Liu 10377 (IBSC)	–

for the supra-generic groups. Furthermore, the homology of synapomorphies supporting these groups needs to be explored through optimization of lemma micromorphological characters onto molecular cladograms of Chloridoideae (De Pinna, 1991).

The present study aims to: (1) examine lemma micromorphological data for representatives of Chloridoideae, (2) discuss phylogenetic implications for the taxonomy of Chloridoideae, and (3) assess synapomorphies supporting supra-generic groups within the Chloridoideae.

2. Materials and methods

The lemma abaxial surfaces from the proximal florets in spikelets of 83 taxa representing 61 genera of Chloridoideae were observed using a Jeol JSM-6360V scanning electron microscope (Table 1). Data of 27 taxa representing 19 genera from previous publications (Zuloaga, 1986; Valdés-Reyna and Hatch, 1991; Columbus, 1996; Snow, 1996) was reviewed. Sampling was aimed at covering the major supra-generic groups within Chloridoideae (Clayton and Renvoize, 1986; Soreng et al., 2009; Peterson et al., in review). Three specimens of most taxa were studied, while a scanning electron micrograph of each taxon was used to score relevant characters (Tables 2 and 3). Where possible, micrographs have the lemma tip towards the right. No attempt was made to measure quantify variation of the

characters (except in the discussion of distribution frequency) because we only focused on presence or absence of characters. Terminology follows Amarasinghe and Watson (1988, 1991) and Snow (1996).

The molecular matrix of 51 taxa was downloaded from TreeBASE web (<http://www.treebase.org/treebase>) (Columbus et al., 2007). The lemma micromorphological characters were optimized onto the strict consensus tree inferred from WinClada version 1.00.08 (Nixon, 2002) running NONA version 2.00 (<http://www.cladistics.com>) as a son process. In the NONA analysis, three sequential parsimony ratchet runs were chosen, and each replicate included 200 iterations with 20 trees held in memory.

3. Results

3.1. Lemma micromorphology

Eight sets of diagnostic characteristics of the lemma micromorphology in the subfamily Chloridoideae are recognized: (1) long cell outline straight, U-shaped, V-shaped or Ω -shaped (Fig. 16); (2) cork cell semi-circle-shaped, scalariform, crescent-shaped, nodular, or oblong (Figs. 7–11); (3) stomata subsidiary cells triangular, semi-circle-shaped, or rectangular (Figs. 12–17); (4) bicellular microhairs panicoid-type, enneapogonoid-

Table 2
Lemma micromorphological characters and character states used in this study.

No.	Char.	Char. state
1	Long cell outline (LC)	0=straight, 1=U-shaped, 2=V-shaped, 3= Ω -shaped, 4=?
2	Cork cell (CC)	0=absent, 1=semi-circle-shaped, 2=scalariform, 3=crescent-shaped, 4=nodular, 5=oblong, 6=?
3	Stomata subsidiary cell (ST)	0=absent, 1=triangular, 2=semi-circle-shaped, 3=rectangular, 4=?
4	Bicellular microhairs (BM)	0=absent, 1=long base-cell chloridoid, 2=short base-cell chloridoid, 3=enneapogonoid, P=panicoid
5	Papillae (PA)	0=absent, 1=papillae on long cells, 2=papillae on long and short cells, 3=distal swellings on long cells, 4=?
6	Silica cell (SL)	0=absent, 1=dumbbell-shaped, 2=oblong sinuous, 3=cross-shaped, 4=saddle-shaped, 5=circular
7	Microprickle (PR)	0=absent, 1=a-type, 2=b-type, 3=c-type, 4=d-type, 5=?
8	Macrohair (MA)	0=absent, 1=papillate base, 2=sting-shaped, 3=apiculate, 4=geniculate, 5=?

?=Missing.

Table 3
Data matrix with eight lemma micromorphological characters.

Taxon\char no.	1	2	3	4	5	6	7	8
<i>Aeluropus littoralis</i>	1	2	0	4	1	1	2	0
<i>A. littoralis</i> subsp <i>sinensis</i>	1	2	0	4	1	1	2	0
<i>Acrachne racemosa</i>	2	5	1	1	1	1	0	0
<i>Aegopogon cenchroides</i> ^a	2	5	?	1	1	5	3	2
<i>Apochiton burtii</i>	0	5	0	1	1	0	0	0
<i>Astrebula pectinata</i>	2	3	0	1	1	2	0	2
<i>Bewsia biflora</i>	1	1	0	2	0	0	1	0
<i>Blepharidachne tricholepis</i> ^b	0	0	0	1	0	0	1	0
<i>Bouteloua aristidoides</i> ^a	1	2	0	1	1	0	?	2
<i>B. curtispindula</i>	1	2	0	1	3	4	1	3
<i>B. dactyloides</i> ^a	1	2	0	1	3	4	1	2
<i>Brachyachne patentiflora</i>	1	1	1	2	0	0	0	0
<i>Chloris barbata</i>	0	4	0	2	0	0	3	0
<i>C. formosana</i>	0	4	0	2	0	0	3	0
<i>C. gayana</i>	0	4	0	2	0	0	3	0
<i>C. schoenoides</i> ^b	2	0	1	1	3	0	1	3
<i>C. virgata</i>	0	4	0	2	0	0	3	0
<i>C. latisquamea</i>	0	4	0	2	0	0	3	0
<i>C. paniculata</i> ^c	1	3	0	2	0	0	3	2
<i>Chrysochloa hindsii</i>	1	1	3	2	0	0	0	0
<i>Coelachyrum longiglume</i>	2	5	0	4	3	0	0	0
<i>Crypsis aculeata</i>	2	0	1	1	3	0	1	3
<i>Ctenium newtonii</i>	2	3	0	2	0	2	0	0
<i>Cynodon arcuatus</i>	1	5	3	2	0	0	3	3
<i>Dactyloctenium australe</i>	2	5	1	1	1	1	0	0
<i>D. polycarpa</i>	1	5	0	1	2	0	1	0
<i>D. aegyptium</i>	0	5	1	1	1	1	0	0
<i>Daknopholis boivinii</i>	1	5	1	2	0	2	3	2
<i>Desmostachya bipinatifolia</i>	1	5	0	1	0	4	3	0
<i>Dignathia gracilis</i>	2	3	1	2	0	4	0	0
<i>Dinebra retroflexa</i>	1	5	0	1	2	0	1	2
<i>Distichlis spicata</i>	1	5	?	4	2	1	2	2
<i>Drake-Brockmania somalensis</i>	1	2	0	1	1	0	2	0
<i>Eragrostis atrovirens</i>	1	4	0	1	0	0	1	0
<i>E. cilianensis</i>	1	4	0	1	0	0	1	0
<i>E. ciliata</i>	1	4	0	1	0	0	1	0
<i>E. coracana</i>	2	5	1	1	1	1	0	0
<i>E. cylindrica</i>	1	4	0	1	0	0	1	0
<i>E. tenella</i>	1	4	0	1	0	1	1	0
<i>Ectrosia leporina</i> ^c	0	5	0	4	0	1	1	0
<i>Eleusine indica</i>	2	5	1	1	1	1	0	0
<i>Enneapogon desvauxii</i>	1	4	1	3	0	0	1	2
<i>Enteropogon dolichostachyus</i>	2	3	0	2	3	0	0	0
<i>Eragrostiella bifaria</i>	1	4	0	1	0	4	0	2
<i>Erioneuron avenaceum</i> ^b	3	5	?	2	?	1	3	?
<i>Eustachys tenera</i>	3	3	0	2	0	0	0	4
<i>Farrago racemosa</i>	0	5	0	2	0	3	0	0
<i>Fingerhuthia africana</i>	0	4	1	1	1	1	0	0
<i>Gouinia latifolia</i> ^b	1	5	0	2	0	0	1	2
<i>Gymnopogon ambiguus</i> ^b	2	3	0	2	1	0	0	3
<i>Habrochloa bullockii</i>	0	4	0	4	0	0	0	0
<i>Halopyrum mucronatum</i>	1	1	0	1	2	1	0	0
<i>Harpachne schimperii</i>	1	4	0	4	0	1	2	0
<i>Cleistogenes caespitosa</i>	0	1	1	0	0	0	2	2
<i>C. chinensis</i>	0	1	1	0	0	0	2	2
<i>C. hackelii</i>	0	1	1	0	0	0	2	2
<i>C. longiflora</i>	0	1	1	0	0	0	2	2
<i>Leptocarydion vulpiastrum</i>	1	1	0	1	0	1	0	0
<i>Leptochloa chinensis</i>	2	4	0	1	0	0	0	4
<i>L. dubia</i> ^c	0	3	0	1	0	0	2	2
<i>L. fusca</i>	2	5	0	1	2	0	2	0
<i>L. panicea</i> ^c	1	5	0	1	1	0	1	2
<i>Leptothrium senegalense</i>	2	3	0	2	0	4	0	0
<i>Lepturus repens</i>	2	3	0	1	1	4	0	0

Table 3 (continued)

Taxon\char no.	1	2	3	4	5	6	7	8
<i>Lintonia nutans</i>	2	3	0	1	0	0	0	2
<i>Microchloa altera</i>	2	3	0	2	0	0	0	0
<i>M. indica</i>	1	5	3	2	0	2	0	0
<i>Melanocenchris abyssinica</i> ^a	0	1	3	1	1	3	2	3
<i>Muhlenbergia curvitaristata</i>	1	5	0	1	1	3	0	0
<i>M. japonica</i>	1	5	0	1	1	3	0	0
<i>Munroa squarrosa</i> ^b	2	0	0	2	2	0	4	2
<i>Neobouteloua lophostachya</i> ^a	0	3	0	1	2	?	?	4
<i>Neyraudia reynaudiana</i>	0	4	0	4	0	0	2	0
<i>Odyssea paucinervis</i>	0	4	0	1	1	1	2	0
<i>Orinus thoroldii</i>	2	2	0	0	1	1	2	2
<i>Oropetium thomaeum</i>	0	0	0	1	1	0	2	0
<i>Pereilema crinitum</i> ^b	2	0	0	1	1	0	3	0
<i>Pleuraphis jamesii</i> ^a	3	5	?	1	1	1	3	?
<i>Pogonarthria squarrosa</i>	1	4	0	1	0	1	0	0
<i>Pogoneura biflora</i>	2	5	0	1	0	2	0	0
<i>Psilolemma jaegeri</i>	0	1	0	1	0	5	0	0
<i>Redfieldia flexuosa</i> ^b	0	0	0	2	0	0	4	2
<i>Schaffnerella gracilis</i> ^a	2	1	0	2	1	?	2	2
<i>Schmidtia pappophoroides</i>	2	3	1	3	0	0	1	4
<i>Schoenefeldia transiens</i>	1	0	1	2	0	2	0	0
<i>Scleropogon brevifolius</i> ^c	?	?	0	1	1	?	?	2
<i>Sohnsia filifolia</i> ^c	?	?	0	1	0	?	0	0
<i>Spartina alterniflora</i>	2	0	1	2	0	0	3	3
<i>S. anglica</i>	2	0	1	2	0	0	3	2
<i>Sporobolus fertilis</i>	1	5	0	4	0	3	0	0
<i>S. tenuissimus</i>	1	5	0	4	0	3	0	0
<i>S. virginicus</i>	1	5	0	4	0	3	0	0
<i>Tetrachaete elionuroides</i>	0	4	0	2	0	3	0	2
<i>Tetrapogon tenellus</i>	2	3	0	1	1	0	0	0
<i>Tragus australianus</i>	2	2	0	2	2	5	4	1
<i>T. berteronianus</i>	2	2	0	2	2	5	4	1
<i>Trichoneura ciliata</i>	2	1	0	1	0	0	0	0
<i>T. elegans</i> ^b	2	3	0	2	0	0	0	1
<i>Tridens muticus</i> ^b	3	5	?	2	1	2	0	0
<i>Triodia irritans</i>	1	3	1	1	1	1	1	0
<i>T. lanata</i>	1	3	1	1	1	1	1	0
<i>Triplasis americana</i> ^c	?	?	0	1	0	0	2	2
<i>Tripogon chinensis</i>	0	4	0	1	0	0	2	0
<i>Triraphis schinzii</i>	0	4	1	4	0	1	0	2
<i>Uniola paniculata</i>	3	4	1	1	1	1	0	0
<i>Vaseyochloa multinervosa</i> ^b	0	5	0	2	1	4	0	4
<i>Zoysia japonica</i>	2	3	0	2	0	4	0	0
Outgroup								
<i>Panicum hirticaule</i> ^d	1	5	1	4	1	1	0	1

Character number (char no.): 1=long cell outline; 2=cork cell; 3=stomata; 4=bicellular microhair; 5=papillae; 6=silica cell; 7=micropickles; 8=macrohairs. Previous publications: ^aFrom Columbus (1996); ^bFrom Valdés-Reyna and Hatch (1991); ^cFrom Snow (1996); ^dFrom Zuloaga 1986). Character states obtained in this study are in bold.

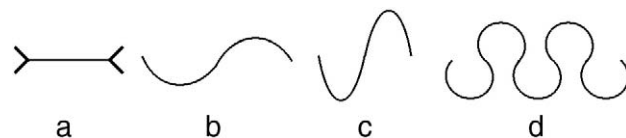


Fig. 1. Basic patterns of anticlinal walls as seen in surface view (adapted from Metcalfe and Chalk, 1979). (a) Outline straight; (b) Outline curved, wide U-shaped curves of shallow amplitude; (c) Outline curved, V-shaped curves of deep amplitude; (d) Outline tightly curved, Ω-shaped curves of deep convolutions.

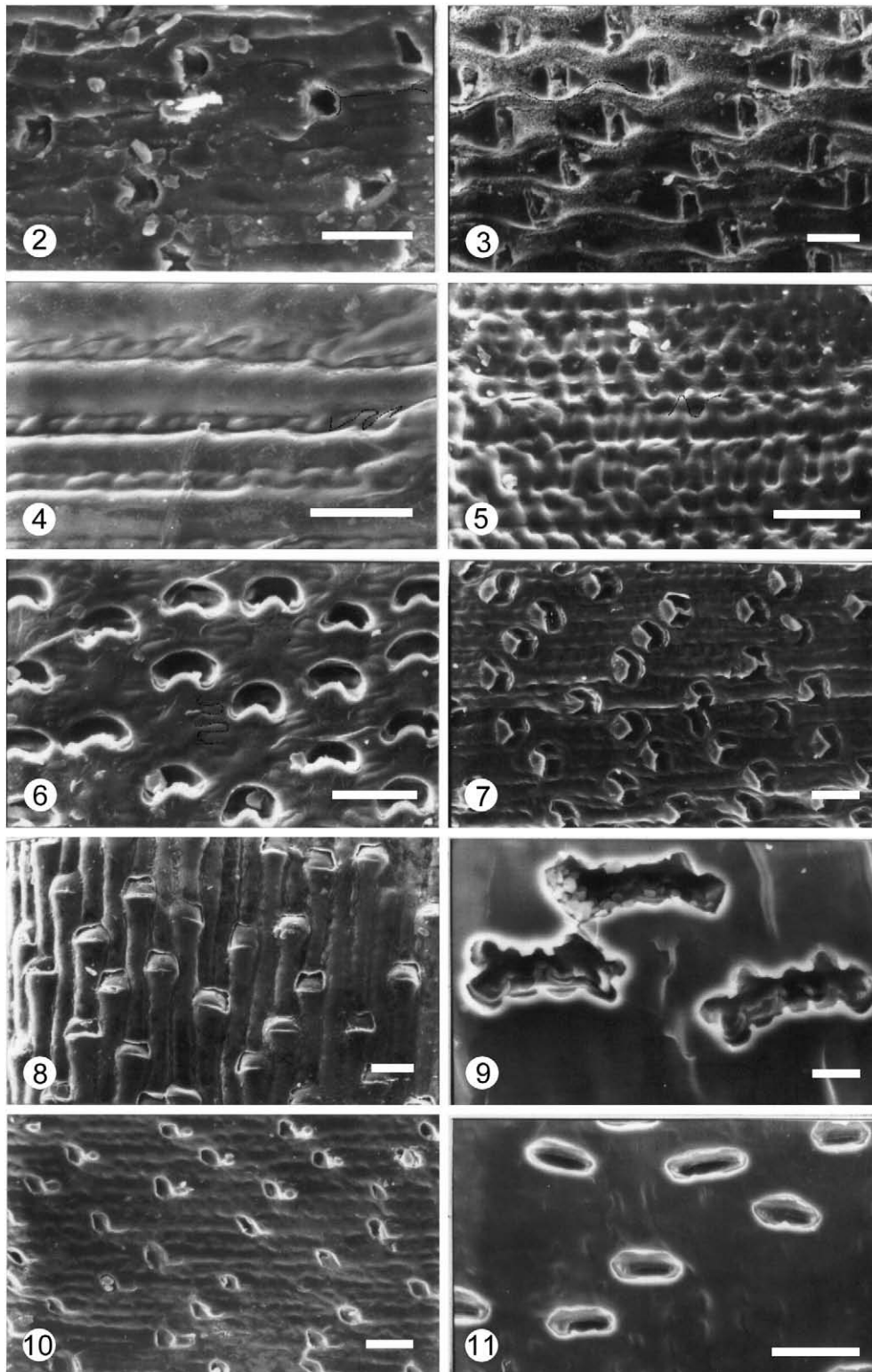


Fig. 2–11. Long cells and cork cells in the lemma of Chloridoideae. (2) *Cleistogenes longiflora*, intercostal long cells outline straight, with semi-circle-shaped cork cells. (3) *Bouteloua curtipendula*, intercostal long cells outline curved, wide U-shaped, with scalfariform cork cells. 4–5 Intercostal long cells outline V-shaped (4) *Spartina alterniflora*. (5) *Crypsis aculeata*. (6) *Eustachys tenera*, intercostal long cells outline deep convolution of omega shape with crescent-shaped cork cells. (7) *Schmidtia pappophoroides*, with crescent-shaped cork cells. 8–9 Nodular cork cells. (8) *Eragrostis cilianensis*. (9) *Enneapogon desvauxii*. 10–11 Oblong cork cells. (10) *Leptochloa fusca*. (11) *Pogoneura biflora*. Scale bars: 2, 4–6, 11, 20 μ m; 46, 7–10, 10 μ m. Dotted line indicated long cell outline.

type or chloridoid-type (including long base-cell and short base-cell subtypes) (Figs. 18–27); (5) papillae on long and short cells, on long cells, or distal swellings on long cells (Figs. 28–35); (6) silica cells dumb-bell-shaped, oblong-sinuous, cross-shaped, saddle-shaped or circular (Figs. 36–43); (7) microprickles a-, b-, c-, or d-type (Figs. 44–50); (8) macrohairs papillate-base, sting-shaped, apiculate, or geniculate (Figs. 51–60). For comparison, the lemma microcharacters of an additional 27 taxa were supplied in Table 3. Full characterization of lemma micromorphology of a few large genera such as *Eragrostis* and *Sporobolus* awaits further study.

3.1.1. Long cells

Intercoastal long cell outlines fall into four types (Fig. 1a–d), following the classification of Metcalfe and Chalk (1979): (a) outline straight in *Cleistogenes longiflora* (Fig. 2); (b) outline curved, wide U-shaped in *Bouteloua curtipendula* (Fig. 3) the type occurs the most frequently here; (c) outline loose, V-shaped in *Spartina alterniflora* (Fig. 4) and *Crypsis aculeata* (Fig. 5); (d) outline tight, Ω -shaped only in *Uniola paniculata* and *Eustachys tenera* (Fig. 6).

3.1.2. Cork cells

These cells were nearly isodiametric and shorter than long cells. They occurred in axial rows (Figs. 7–10) or were oc-

asionally solitary (Fig. 11). They were more frequent in the costal zones than in the intercostal zones. The five types of cork cell shapes were: semi-circle-shaped in *C. longiflora* (Fig. 2); scalariform in *Bouteloua curtipendula* (Fig. 3); crescent-shaped in *Eustachys tenera* (Fig. 6) and *Schmidtia pappophoroides* (Fig. 7); nodular in *Eragrostis cilianensis* (Fig. 8) and *Enneapogon desvauxii* (Fig. 9); oblong in *Leptochloa fusca* (Fig. 10) and *Pogoneura biflora* (Fig. 11).

3.1.3. Stomata

Paracytic stomata occurs in the Chloridoideae (Carpenter, 2005). They were distributed throughout the intercostal zones of rows parallel to the long cells. Three stomata shapes were found: triangular in *Dactyloctenium aegyptium* (Fig. 12); semi-circle-shaped in *Cleistogenes longiflora* (Fig. 13) and *Triodia irritans* (Fig. 14); rectangular in *Microchloa indica* (Fig. 15), *Cynodon arcuatus* (Fig. 16), and *Spartina alterniflora* (Fig. 17).

3.1.4. Bicellular microhairs

These hairs were generally scattered in the intercostal zones near the lemma tip. Three of the microhair types were found in Chloridoideae (Amarasinghe and Watson, 1988): panicoid-type of relatively narrow cap cells in *Neyraudia reynaudiana* (Kunth) Keng ex Hitchc. (Figs. 18); enneapogonoid-type of relatively long base cells in *Schmidtia pappophoroides*

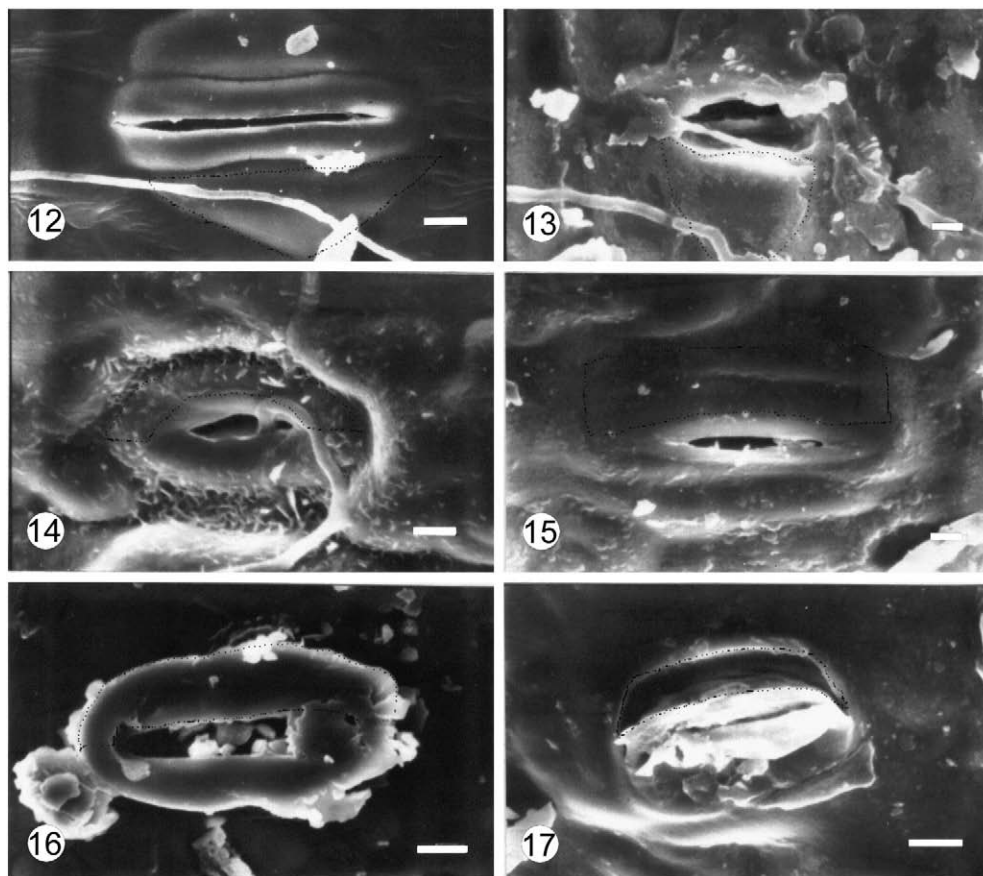


Fig. 12–17. Stomata in the lemma of Chloridoideae. (12) *Dactyloctenium aegyptium*, triangular subsidiary cells of stomata. 13–14 Semi-circle-shaped subsidiary cells of stomata. (13) *Cleistogenes longiflora*. (14) *Triodia irritans*. 15–17 Rectangular subsidiary cells of stomata. (15) *Microchloa indica*. (16) *Cynodon arcuatus*. (17) *Spartina alterniflora*. Scale bars: 12, 14–17, 2 μ m; 13, 1 μ m.

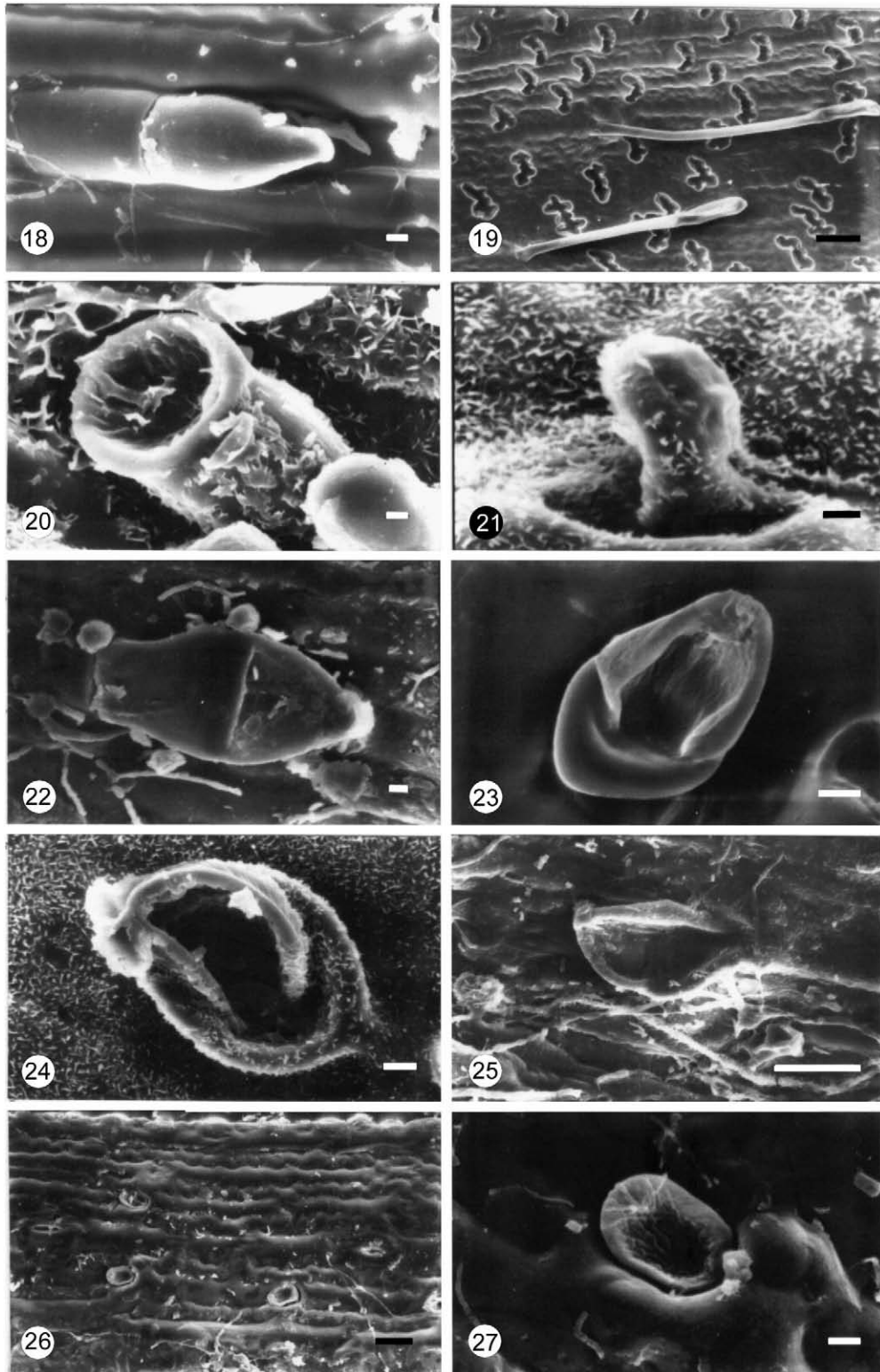


Fig. 18–27. Bicellular microhairs in the lemma of Chloridoideae. (18) Panicoid-type in *Neyraudia reynaudiana*. (19) Enneapogonoid-type in *Schmidtia pappophoroides*. 20–22 Long base-cell chloridoid-type. (20) *Odyssea paucinervis*. (21) *Drake-Brockmania somalensis*. (22) *Tripogon chinensis*. 23–27. Short base-cell chloridoid-type. (23) *Bewsia biflora*. (24) *Chloris latisquamea*. (25) *Zoysia japonica*; (26) *Microchloa indica*. (27) *Spartina alterniflora*. Scale bars: 18, 20–25, 27, 2 μm ; 19, 10 μm ; 26, 20 μm .

(Figs. 19); chloridoid-type of hemispherical cap cells in *Odyssea paucinervis* (Figs. 20), *Drake-Brockmania somalensis* (Fig. 21), *Tripogon chinensis* (Fig. 22), *Bewsia biflora*

(Fig. 23), *Chloris latisquamea* (Fig. 24), *Zoysia japonica* (Fig. 25), *Microchloa indica* (Fig. 26), and *Spartina alterniflora* (Fig. 27). Chloridoid-type microhairs can also be classified into

two subtypes: long-base-cell subtype with the cap cell not immersed into the long base cell (Figs. 20–22) and short-base-cell subtype with cap cell immersed into the short base cell (Figs. 23–27).

3.1.5. Papillae

These are short, undifferentiated processes that arise from the outer cell wall. They occurred in three locations of the middle intercostal zones of lemmas in Chloridoideae: on long and short cells in *Distichlis spicata* (Fig. 28) and *Leptochloa fusca* (Fig. 29); on long cells in *Orinus thoroldii* (Fig. 30), *Triodia irritans* (Fig. 31), *Apochiton burtii* (Fig. 32), and *Aeluropus*

littoralis (Fig. 33); on the distal portion of long cells in *Coelachyrum longiglume* (Fig. 34) and *Enteropogon dolichostachyus* (Fig. 35).

3.1.6. Silica cells

These cells were filled with a single silica body. They occurred more frequently in costal zones than in intercostal zones, and are single row (Figs. 36–39), or solitary (Figs. 40–43). Five different shapes of silica cells were found: dumb-bell in *Uniola paniculata* (Fig. 36), *Fingerhuthia africana* Lehm. (Fig. 37), and *Dactyloctenium aegyptium* (Fig. 38); oblong-sinuuous in *Microchloa indica* (Fig. 39); cross-shaped in

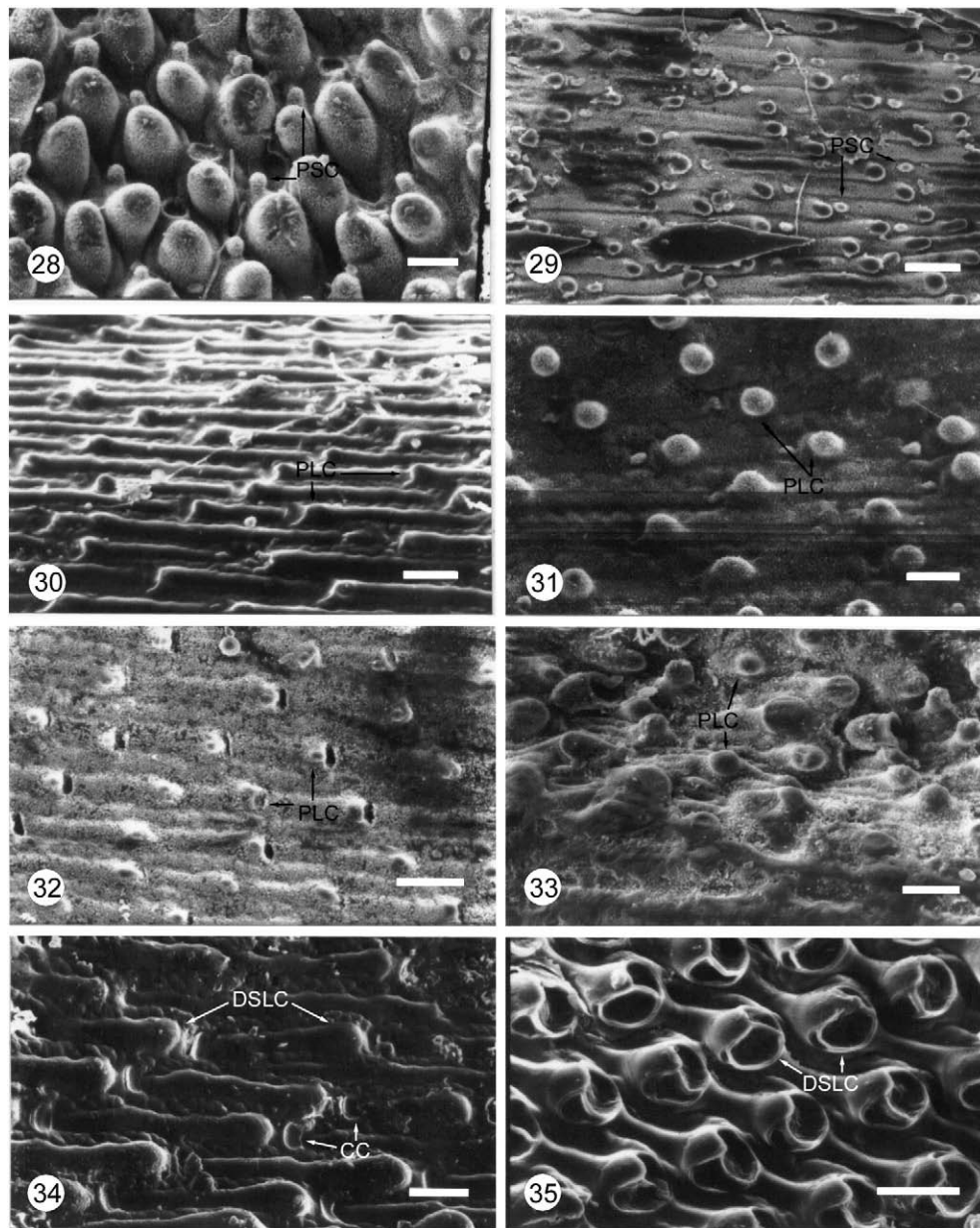


Fig. 28–35. Papillae in the lemma of Chloridoideae. 28–29 Papillae on long and short cells. (28) *Distichlis spicata*. (29) *Leptochloa fusca*. 30–33 Papillae on long cells. (30) *Orinus thoroldii*. (31) *Triodia irritans*. (32) *Apochiton burtii*. (33) *Aeluropus littoralis*. 34–35 Distal swellings on long cells. (34) *Coelachyrum longiglume*. (35) *Enteropogon dolichostachyus*. Scale bar: 10 μ m. Abbreviations: PLC, papilla on long cell; PSC, papillae on long and short cells; DSL, distal swelling on long cell; CC, cork cell.

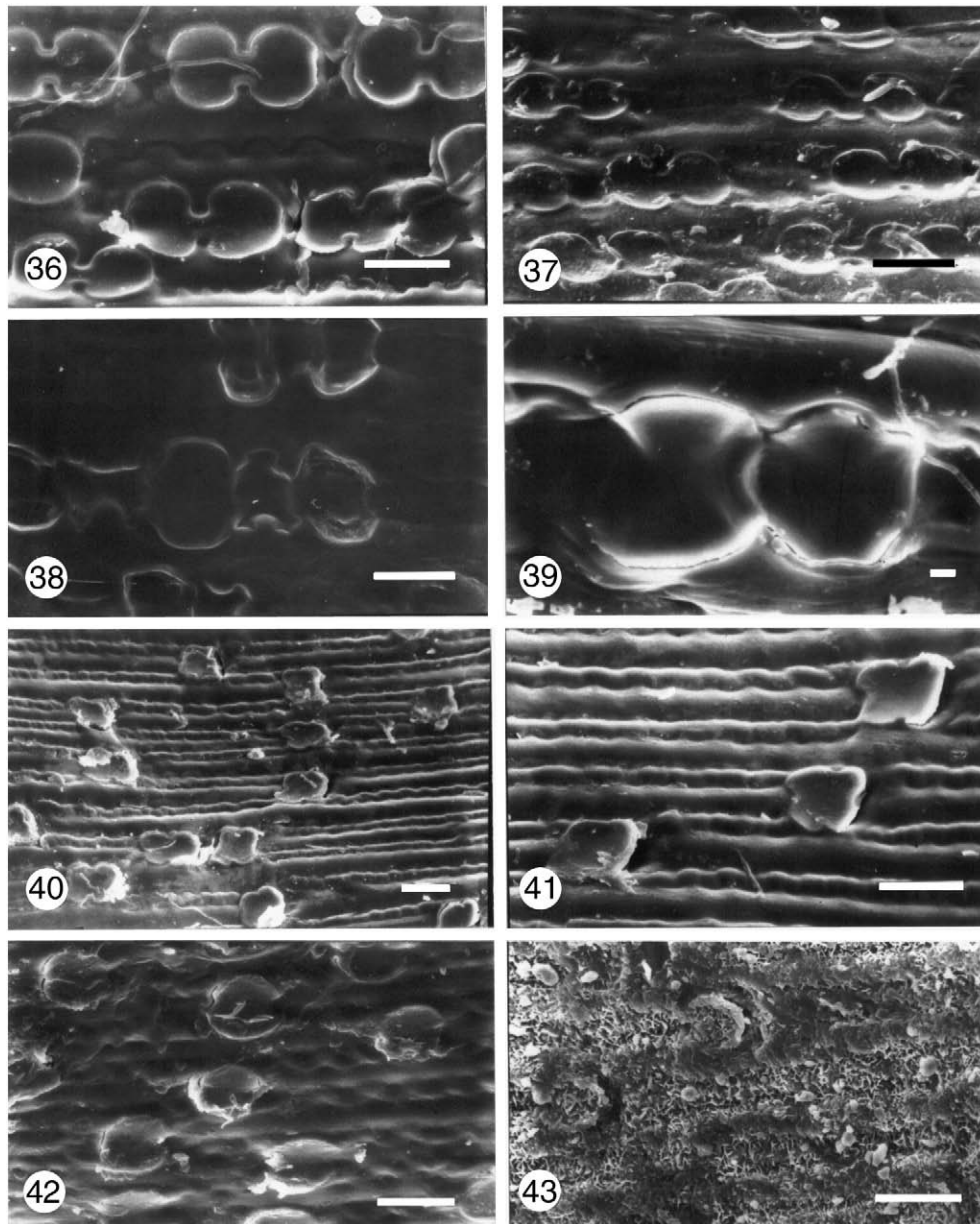


Fig. 36–43. Silica cells in the lemma of Chloridoideae. 36–38 Dumb-bell-shaped silica cells. (36) *Uniola paniculata*. (37) *Fingerhuthia africana*. (38) *Dactyloctenium aegyptium*. (39) Oblong sinuous silica cell in *Microchloa indica*. 40–41 Cross-shaped silica cells. (40) *Sporobolus tenuissimus*. (41) *S. virginicus*. (42) Saddle-shaped silica cells in *Desmostachya bipinnata*. (43) Circular silica cells in *Psilolemma jaegeri*. Scale bars: 36–38, 41, 43, 10 μm ; 39, 2 μm ; 40, 20 μm . Abbreviations: SC, silica cells.

Sporobolus tenuissimus (Fig. 40) and *S. virginicus* (Fig. 41); saddle-shaped in *Desmostachya bipinnata* (Fig. 42); and circular obscured by epicuticular waxes in *Psilolemma jaegeri* (Fig. 43). We found the dumb-bell-shaped silica cells in *Lepidocarydion* (Valdés-Reyna and Hatch, 1991; Piperno and Pearsall, 1998) that were not observed by Snow (1996).

3.1.7. Microprickles

These swollen processes arising from zones in both the costal and intercostal zones, increased in frequency from the base to the lemma tip. Four types of microprickles (Fig. 44) were observed: (a) straight sided (Fig. 45); (b) sides straight with tip

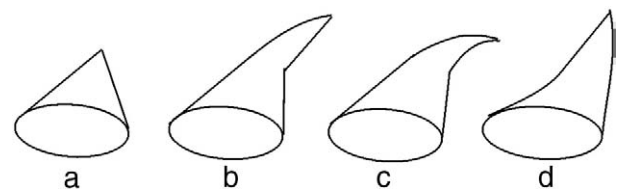


Fig. 44. Microprickle diagrams in lemma of Chloridoideae (adapted from Ellis, 1979). (a) Barbs developed basally from the apex of the base; (b) Barb with direct point not developed from the apex of the base; (c) Barb with recurved point not developed from the base; (d) Barb with contrarily recurved point not developed from the apex of the base.

at the microprickle center and angle to the base (Figs. 46 and 47); (c) sides curved with tip deflected away from the microprickle center (Fig. 48); and (d) sides curved towards the microprickle center (Figs. 49 and 50).

3.1.8. Macrohairs

These are unicellular structures visible in *Enneapogon desvauxii* (Fig. 51) and *Tetrachaete elionuroides* Chiov. (Fig. 52). They occurred in the intercostal zones, but were more commonly found over the costal zones or at the lemma margin with variation in length and flexibility. Four types of macrohairs are found: papillae-based in *Tragus australianus* S. T. Blake (Figs. 53 and 54); sting-shaped in *C. hackelii* (Fig. 55) and *C. chinensis* (Fig. 56); apiculate in *C. aculeate* (Fig. 57) and *Spartina alterniflora* (Fig. 58); geniculate in *Eustachya tenera* (Fig. 59) and *Leptochloa chinensis* (Fig. 60).

3.2. Phylogenetic implications of lemma micromorphological characters and homology assessment for synapomorphies

Eight lemma micromorphological characters were informative when mapped onto a strict consensus tree of molecular data

(Columbus et al., 2007), genera were substituted for species in Fig. 61. Shared lemma micromorphological characters indicated that they are reliable phylogenetic markers at the generic level in Chloridoideae (Snow, 1996).

The Chloridoideae was not defined by any lemma morphological characters, but seven supra-generic groups were newly defined by lemma micromorphological characters in Fig. 61: *Enneapogon–Eragrostis* was defined by straight outline long cells (char. 1:0), *Fingerhuthia–Uniola* was defined by semi-circle-shaped stomata (char. 3:2), *Zoysia–Spartina* was defined by V-shaped outline long cells (char. 1:2), *Sporobolus–Spartina* was defined by lacking cork cells and papillae (chars 2:0 and 5:0), *Erioneuron–Pleuraphis* was defined by c-type microprickles (char. 7:3), *Triodia–Leptochloa* was defined by straight outline long cells (char. 1:0) and crescent-shaped cork cells (char. 2:3), *Dactylocteniumaeg–Neobouteloua* was defined by straight outline long cells (char. 1:0), *Enteropogonmol–Microchloa* was defined by crescent-shaped cork cells (char. 2:3) and absent papillae (char. 5:0). Seven characters including straight outline long cells, crescent-shaped cork cells, absent stomata, absent papillae, dumb-bell-shaped silica cells, c-type microprickles, and

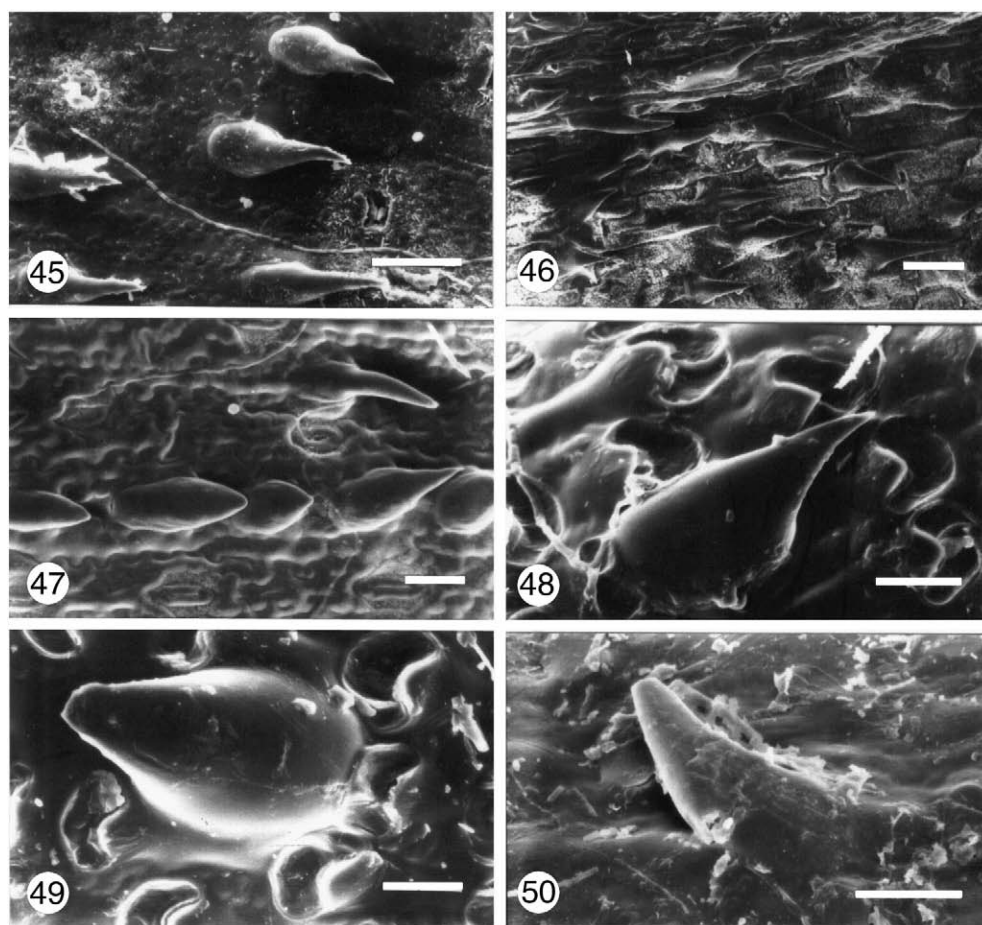


Fig. 45–50. Microprickles of in the lemma of Chloridoideae. (45) a-type of microprickles in *Enneapogon desvauxii*. 46–47 b-type of microprickles. (46) *Cleistogenes longiflora*. (47) *Orinus thoroldii*. (48) c-type of microprickles in *Spartina anglica*. 49–50 d-type of microprickles. (49) *Zoysia japonica*. (50) *Farrago racemosa*. Scale bar: 20 μ m.

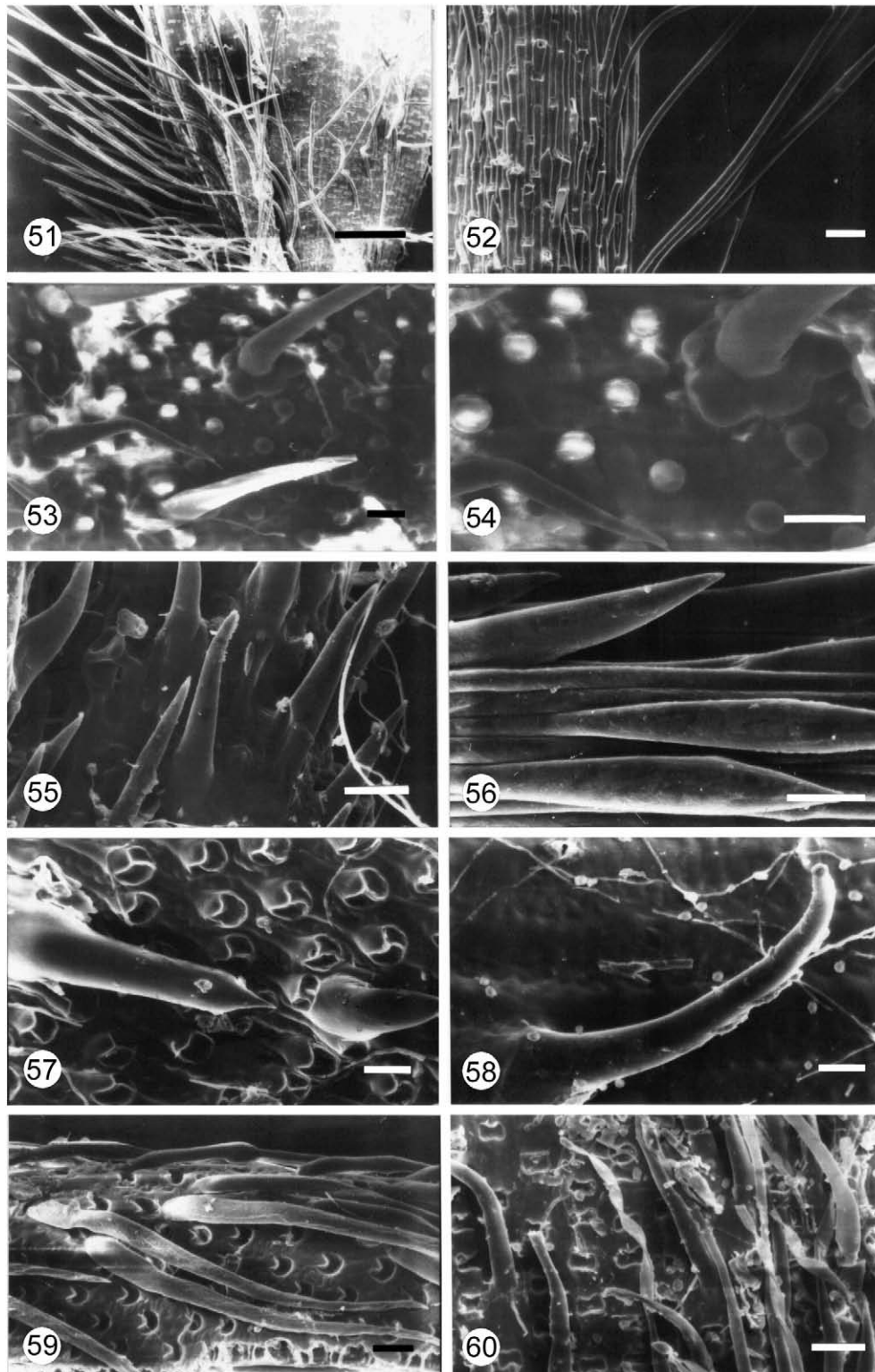


Fig. 51–60. Macrohairs in the lemma of Chloridoideae. 51–52 and 56–57 Sting-shaped macrohairs. (51) *Enneapogon desvauxii*. (52) *Tetrachaete elionuroides*. 53–54 Papilla-base macrohairs. (53) *Tragus australianus*. (54) Close-up of the papilla-base macrohair. (55) *Cleistogenes hackelii*. (56) *Cleistogenes chinensis*. 57–58 Apiculate macrohairs. (57) *Crypsis aculeata*. (58) *Spartina alterniflora*. 59–60 Geniculate macrohairs. (59) *Eustachys tenera*. (60) *Leptochloa chinensis*. Scale bars: 51, 500 μ m; 52, 60, 50 μ m; 53–59, 20 μ m.

papillate-base macrohairs (chars 1:0, 1:2, 2:3, 3:1, 5:0, 6:1, 7:3, and 8:2) are homologous. However, the enneapogonoid-type bicellular microhairs appeared as nonhomoplasious in the Chloridoideae.

4. Discussion

Our study provided two important findings: (1) five exhaustive lemma micromorphological characters are presented in

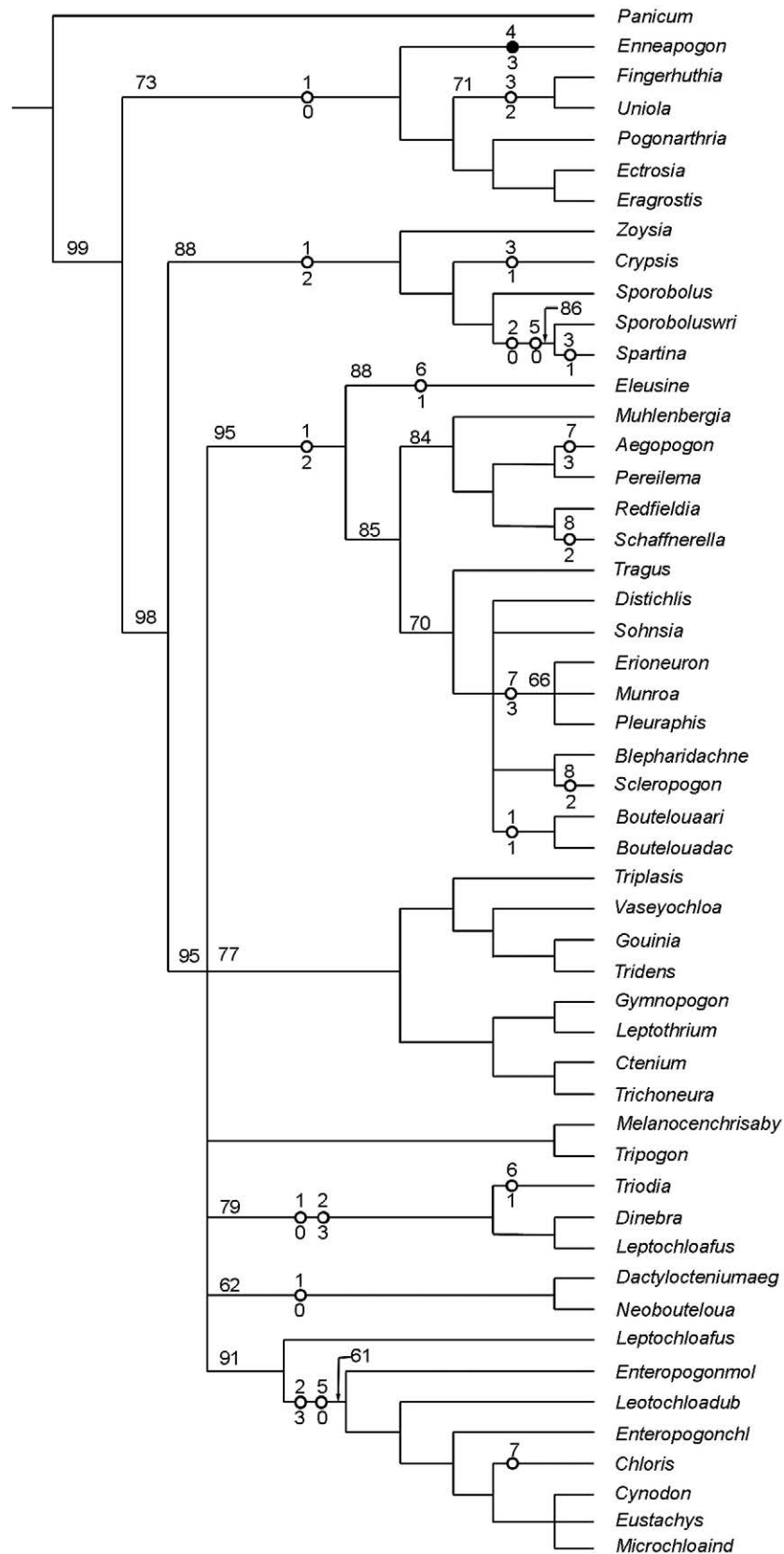


Fig. 10. Lemma micromorphological characters mapped onto the strict consensus tree of molecular data (Columbus et al., 2007). Numbers above branches are bootstrap percentages. Numbers above and below circles are character number and character state (see Tables 2 and 3), respectively. Black circles indicated nonhomoplasious synapomorphies, white circles indicated homoplasious synapomorphies.

Chloridoideae; (2) the phylogenetic implications and homology for eight lemma micromorphological characters are discussed for supra-generic groups of Chloridoideae.

The five exhaustive lemma micromorphological characters and their states are reported here: U-shaped, V-shaped, and Ω -shaped long cell outlines (chars 1:1, 1:2, and 1:3); long base-cell and short base-cell chloridoid bicellular microhairs (chars 4:1 and 4:2); papillae on long and short cells, on long cells, distal swellings on long cells (chars 5:1, 5:2, and 5:3); a-, b-, c-, and d-types microprickles (chars 7:1, 7:2, 7:3, and 7:4); papillate base and sting-shaped macrohairs (chars 8:2 and 8:3).

The optimization of lemma micromorphological characters suggests that these five lemma micromorphological characters (long cells, cork cells, stomata, papillae, and microprickles) are of phylogenetic significance for some supra-generic groups. Three types of long cells occurred universally as phylogenetic markers in the Chloridoideae. The supra-generic group of the *Enneapogon* (Cotteinae) sister to *Fingerhuthia* and *Uniola* (Uniolinae) and *Ectrosia* and *Eragrostis* (Eragrostidinae), circumscribed as a smaller Eragrostideae (Peterson et al., 2007a; Soreng et al., 2009), was supported by straight outline long cells (char.1:0). The supra-generic group of *Zoysia*–*Crypsis*–*Sporobolus*–*Spartina* was positioned in a single tribe in Soreng et al. (2009) and Peterson et al. (in review). *Crypsis* and *Sporobolus* were placed in subtribe Sporobolinae based on rebranched inflorescences and spikelets with single florets (Clayton and Renvoize, 1986); and *Spartina* was placed in Cynodonteae subtribe Chloridinae based on spikelets having single fertile nondeciduous florets arranged along one side and *Zoysia* was positioned in Cynodonteae subtribe Zoysiinae based on its spiciform inflorescence and spikelets having single florets and falling as a single unit. The V-shaped outline long cell (char. 1:2) of lemma supported their close relationship among genera exhibiting morphologically diverse inflorescences. The V-shaped outline long cells (char. 1:2) also occurred in the *Eleusine*–*Bouteloua* group (Fig. 61), whose genera were positioned in the large tribe Cynodonteae of Soreng et al. (2009): *Distichlis* was placed in subtribe Monanthochloinae based on the possession of several disarticulate fertile florets; *Eleusine* was placed in subtribe Eleusininae; *Blepharidachne* and *Scleropogon* were placed in the tribe Cynodonteae, while *Muhlenbergia*, *Aegopogon*, *Pereilema*, *Redfieldia*, and *Schaffnerella* were placed in subtribe Muhlenbergiinae (Peterson et al., 2007b); *Bouteloua* was placed in Cynodonteae based on one fertile floret with additional sterile florets (Peterson et al., 2007b; Peterson et al., in review). The straight outline long cells (char 1:0) also occurred twice in supra-generic groups of *Triodia*–*Dinebra*–*Leptochloa* and *Dactyloctenium*–*Neobouteloua*. Phillips (1973) stated that *Dinebra* is closely related to *Leptochloa* differing in part by its deciduous inflorescence branches. Here we show the character ‘straight long cell outline’ (char 1:0) and ‘crescent-shaped cork cells’ (char 2:3) support her opinion.

The crescent-shaped cork cell (char 2:3) and absent papillae (char 5:0) occurred in *Enteropogon*–*Microchloa* clade. Peterson et al. (in review) placed these genera in the tribe Cynodonteae subtribe Eleusininae based on seven molecular markers. Inflorescences of

the clade bear only nondeciduous primary branches, spikelets arranged along one side, and three-nerved lemmas. With the exception of *Leptochloa dubia* which has multiple fertile florets per spikelet, the clade members share a single fertile floret per spikelet, usually accompanied by one or more sterile upper florets but further sampling of allied genera is required. This distinction led Clayton and Renvoize (1986) to place *Leptochloa* in Eleusininae away from the other members of the subtribe. Another species *Leptochloa fusca* forms a well-supported clade with *Dinebra* as a sister taxon. Additional data are required to critically evaluate relationships between *Chloris* and its near relatives.

The subtribe Uniolinae (Soreng et al., 2009) is a monophyletic assemblage in the *matK*, *trnL-F*, and *ITS* phylogenies of Hilu and Alice (2001). Two genera *Fingerhuthia* and *Uniola* formed a supra-generic group with support of semi-circular stomata subsidiary cells (char 3:2). Snow (1996) stated that stomata appeared as atavisms from the transformationally antecedent leaves; ontogenetic studies of stomata for Chloridoideae will be needed to resolve this question.

Mapping lemma micromorphological characters on a molecular phylogeny is a valuable approach that can provide important information on character evolution. Our morphological data often gave poorly resolved consensus trees with clades of low support. Moreover, the single data set often resulted in artificial groupings which have been alluded to by Hilu and Wright (1982) in their phenetic study of grasses. These factors suggest that mapping morphological character distribution within a phylogenetic context might lead to a more accurate estimation of synapomorphies.

From the phylogenetic distribution of characters, seven lemma micromorphological characters were homoplasious in the Chloridoideae, and only the enneapogonoid-type bicellular microhairs were synapomorphic in *Enneapogon* and *Schmidtia*. This may reflect strong directional selection under environmental control. With respect to lemma homoplasy, microprickles and macrohairs have been reported to accumulate silica which has been associated with a range of effects (Valdés-Reyna and Hatch, 1991).

From the data presented, five characters (long cells, cork cells, stomata, papillae, microprickles) were of phylogenetic significance for the supra-generic groups within the Chloridoideae. Seven characteristics (straight outline long cell, crescent-shaped cork cell, absent stomata, absent papillae, dumb-bell-shaped silica cell, c-type microprickle, and papillate-base macrohair) support the majority of species in the Chloridoideae. Further investigations are needed to explore the ontogeny of lemma micromorphological characters within this subfamily.

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